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Research Article

Lodgepole pine (*Pinus contorta* Douglas ex Loudon) invasion in subarctic Iceland: evidence from a long-term study

Pawel Wasowicz[1], Guðrún Óskarsdóttir[2], Þóra Ellen Þórhallsdóttir[3]

1 *Natural Science Institute of Iceland, Borgir vid Nordurslod, 600 Akureyri, Iceland*
2 *East Iceland Nature Research Centre, Bakkavegur 5, 740 Neskaupstaður, Iceland*
3 *Institute of Life and Environmental Sciences, University of Iceland, Askja, Sturlugata 7, 102 Reykjavík, Iceland*

Corresponding author: Pawel Wasowicz (pawel.wasowicz@natt.is)

Abstract

The North American lodgepole pine (*Pinus contorta*) has been widely introduced globally and is now considered invasive in several countries. It was first planted in subarctic Iceland in the 1950s. Recently, the forestry sector has strongly promoted it as an attractive means of carbon capture to mitigate global climate change. It is now the most extensively planted tree species in Iceland. We describe the expansion of the lodgepole pine from a mid-20th-century plantation in Steinadalur, southeast Iceland, and decadal changes between 2010 and 2021. The extent of occurrence expanded nearly tenfold, with tree number and population density reflecting exponential growth patterns. The lodgepole pine colonised diverse habitats, including native birch woodlands and heathland, and was associated with significant reductions in vascular plant species richness and diversity. We conclude that lodgepole pine has the characteristics of an invasive species in Steinadalur and that this will also apply to many native ecosystems across most lowland regions of Iceland. Our study highlights the urgent need for management strategies to mitigate the long-term ecological impacts of lodgepole pine invasion in subarctic environments.

Key words: Afforestation impacts, biological invasions, Iceland, invasive species, plant diversity, species richness, Subarctic ecosystems

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Introduction

The limited success in reducing greenhouse gas emissions has driven many nations to explore alternative strategies to mitigate global climate change. Large-scale afforestation has emerged as a widely advocated nature-based solution for carbon capture (Andres et al. 2022; Nasi 2022; Portmann et al. 2022). This approach has been adopted as official policy in numerous countries and has spurred extensive private sector initiatives (Seymour 2020).

Afforestation of previously treeless landscapes represents a profound ecological shift, altering key processes such as soil dynamics, hydrology, species composition, plant functional groups, and vegetation structure (Ehrenfeld 2010; Nuñez et al. 2017). To date, carbon-focused afforestation efforts have largely been dominated by monoculture plantations (Seddon et al. 2021; Bukoski et al. 2022), often relying on exotic species, particularly conifers (Tölgyesi et al. 2022). Many of these species could become invasive (Simberloff et al. 2009). For instance, among widely

planted pines (*Pinus* spp.), those most commonly used in plantations are also the species most likely to spread and become invasive (Wyse et al. 2022). Invasive alien species (IAS) are recognized as significant drivers of global biodiversity loss (Isbell et al. 2022) and have adverse effects on ecosystems and human well-being worldwide (Roy et al. 2024). IAS often reduce regional biodiversity and degrade ecosystem services such as water provisioning and erosion control (Simberloff et al. 2009; Andres et al. 2022; Hua et al. 2022).

Predicting the behaviour of newly introduced exotic species can be challenging. However, certain traits—both of invasive species and the ecosystems they invade–are associated with invasion success. Globally, isolated oceanic islands are particularly vulnerable (Pyšek et al. 2020). Species-poor ecosystems, recently disturbed areas, and open habitats are more prone to invasion than species-rich, undisturbed, or closed natural ecosystems (Lembrechts et al. 2016; Beaury et al. 2020; Lannes et al. 2020). Successful invasive species often originate from biodiverse regions where they evolved under intense competition and predation pressures (Fristoe et al. 2023). While the Arctic and Subarctic were historically considered resistant to IAS (Lassuy and Lewis 2013), increasing human activity, trade, and disturbances, combined with rising temperatures, are now exposing these high-latitude regions to greater invasion risks (Wasowicz et al. 2020).

All these vulnerabilities are evident in subarctic Iceland, an isolated North Atlantic island with a species-poor vascular flora. Iceland's only native forest-forming tree species is mountain birch *Betula pubescens* subsp. *tortuosa* (Ledeb.) Nyman (Thórhallsdóttir 2021). Human settlement, approximately 1,150 years ago, led to extensive deforestation, catastrophic erosion, and significant ecosystem and soil loss (Barrio and Arnalds 2022). Forests and woodlands, which may have originally covered over 20–30% of Iceland's 103,000 km^2, were reduced to just 1% by 1900 (Aradóttir and Eysteinsson 2005).

Awareness of Iceland's degraded ecosystems prompted the first restoration efforts in the early 20th century (Olgeirsson 2007). Regular planting of exotic trees began in the 1950s, focusing on conifers: *Picea*, *Pinus*, and *Larix* (Traustason and Snorrason 2008; Eysteinsson 2017). Afforestation intensified in the 1990s with regional initiatives funded by state grants. Today, most projects prioritize exotic conifers over native species. For instance, lodgepole pine (*Pinus contorta* Douglas ex Loudon), Siberian larch (*Larix sibirica* Ledeb.), and spruces: *Picea sitchensis* (Bong.) Carrière and *Picea* × *lutzii* Little dominate plantings, with lodgepole pine alone accounting for 25% of trees planted between 2016 and 2020 (4.3 million trees).

Despite this large-scale planting, research on the invasiveness and spread of lodgepole pine in Icelandic ecosystems remains limited. Native to western North America, lodgepole pine is a fast-growing, hardy species that thrives in environments suboptimal for many other timber trees (Vacek et al. 2022). It has been widely introduced in Europe, Turkey, New Zealand, and South America, where it is recognized as invasive in some regions (Ledgard 2001; Richardson and Rejmánek 2004; Langdon et al. 2010; Taylor et al. 2016). However, little is known about its invasiveness in Europe, including Iceland (Jacobson and Hannerz 2020).

This study presents the evaluation of the invasive potential of lodgepole pine in Iceland. Using the work of Guðmundsdóttir (2012) in Steinadalur, southeastern Iceland, as a baseline, we conducted a decadal analysis to:

1. Examine the patterns, speed, and extent of lodgepole pine spread beyond plantation boundaries.
2. Assess its impact on vascular species richness and diversity.
3. Assess population densities and early ecosystem impacts in invaded areas.
4. Evaluate whether lodgepole pine should be classified as an invasive species in Iceland.

Methods

The study species

Lodgepole pine is native to the western part of North America, occurring from SW Alaska and Yukon to Utah, Colorado, and the Mexican state of Baja California (Karl 1993). The species has also been intentionally introduced worldwide. In New Zealand, lodgepole pine was introduced for commercial purposes and for erosion control (Richardson 1998). In northern Europe, lodgepole pine was widely planted because it presented a higher yield per ha and faster growth than the native Scots pine (*Pinus sylvestris* L.) (Karlman 1981). In Iceland, the species has been repeatedly imported for forestry since the first half of the 20th century. Trees originating from the Skagway region are now the most widespread in Icelandic plantations (Sigurgeirsson 1988). The Icelandic plants are likely to be hybrids between *P. contorta* Douglas ex Loudon subsp. *contorta* and *P. contorta* subsp. *latifolia* Engelm. ex S. Watson (Rudolf and Lapp 1987).

Lodgepole pine has a wide ecological amplitude, and is well adapted to survive and reproduce in harsh environments (Wheeler and Guries 1982). Within its native range, it grows from near sea level to an altitude of 3,350 m a.s.l., and from the mild but cool and rainy Pacific coast to the cold and continental interior of the northern Rocky Mountains (Critchfield 1957). In its native range, lodgepole pine grows in a wide variety of topographic settings from flat plains to steep slopes and rocky ridges (Pfister and Daubenmire 1975). It tolerates a wide spectrum of soil conditions including both dry and wet, fertile and poor soils and even bare gravel (Despain 2001; Elfving et al. 2001).

The lodgepole pine's ability to thrive across diverse ecological conditions, regenerate post-fire, and rapidly mature early in its life cycle are essential factors enabling it to play a wide array of successional roles (Elfving et al. 2001). On poor soils, the species can become dominant and represent the final climax stage, forming extensive monotypic stands (Timber Management Research Forest Service 1979).

Lodgepole pine has several life history traits that make it potentially highly invasive. These include small seed mass (<50 mg), short juvenile period (<10 years) and short interval between large seed crops. Small seed mass allows larger numbers of seeds produced, better dispersal, higher initial germinability, and shorter chilling period needed to overcome dormancy, whereas a short juvenile period and short interval between large seed crops translate into early and high recruitment (Richardson and Rejmánek 2004). These advantages facilitated the invasion of lodgepole pine in many countries where it had been introduced by humans (Ledgard 2001; Langdon et al. 2010; Jacobson and Hannerz 2020).

Study site and climate

Steinadalur is a short (2 km) but relatively wide (1.7 km) valley about 3 km inland from the coast in SE Iceland. The valley (ca. 40 m a.s.l.) is open to the east but otherwise surrounded by mountains reaching up to 600 m a.s.l. The bottom of the valley is flat and has been filled with sediment (gravel and stones) by the glacial river Kaldakvísl. The surrounding mountains are largely covered by birch woodland (*B. pubescens* subsp. *tortuosa*) to an elevation of about 200 m a.s.l. The higher parts of the slopes are mostly dominated by heath and grassland vegetation, which is also patchily present in the lower parts of the valley (Fig. 1).

The plantation in Steinadalur consisting of lodgepole pine and Sitka spruce (*Picea sitchensis*) was initiated in 1959 and expanded to ca. 0.02 km^2 in 1961 (Guðmundsdóttir 2012). The first records of lodgepole pine spread beyond the original plantation date from 1985 (Guðmundsdóttir 2012).

There is no weather station in Steinadalur, but climate stations are located 45 km to the SW (Fagurhólsmýri) and 40 km to the NE (Höfn) and the similarity of their climate suggests that they are a good proxy for Steinadalur. The regional climate is highly oceanic with annual precipitation well over 1,500 mm and exceeding 100 mm in most months (unpublished data from the Icelandic Met Office). The average annual temperature (2000–2020) was 5.3 °C and 5.5 °C at Höfn and Fagurhólsmýri respectively, mean temperature of the warmest month was 13 °C and 14 °C, while that of the coldest month was -1.5 °C and -1.9 °C, respectively (see Suppl. material 1). The frost-free period for both stations was ca. 4 months, from June to September. It is almost certain that due to specific orographic conditions in Steinadalur, microclimatic conditions differ from Fagurhólsmýri and Höfn, but we do not expect these differences to be pronounced. The prevailing winds in the Steinadalur valley are from the northwest (Icelandic Met Office 2022).

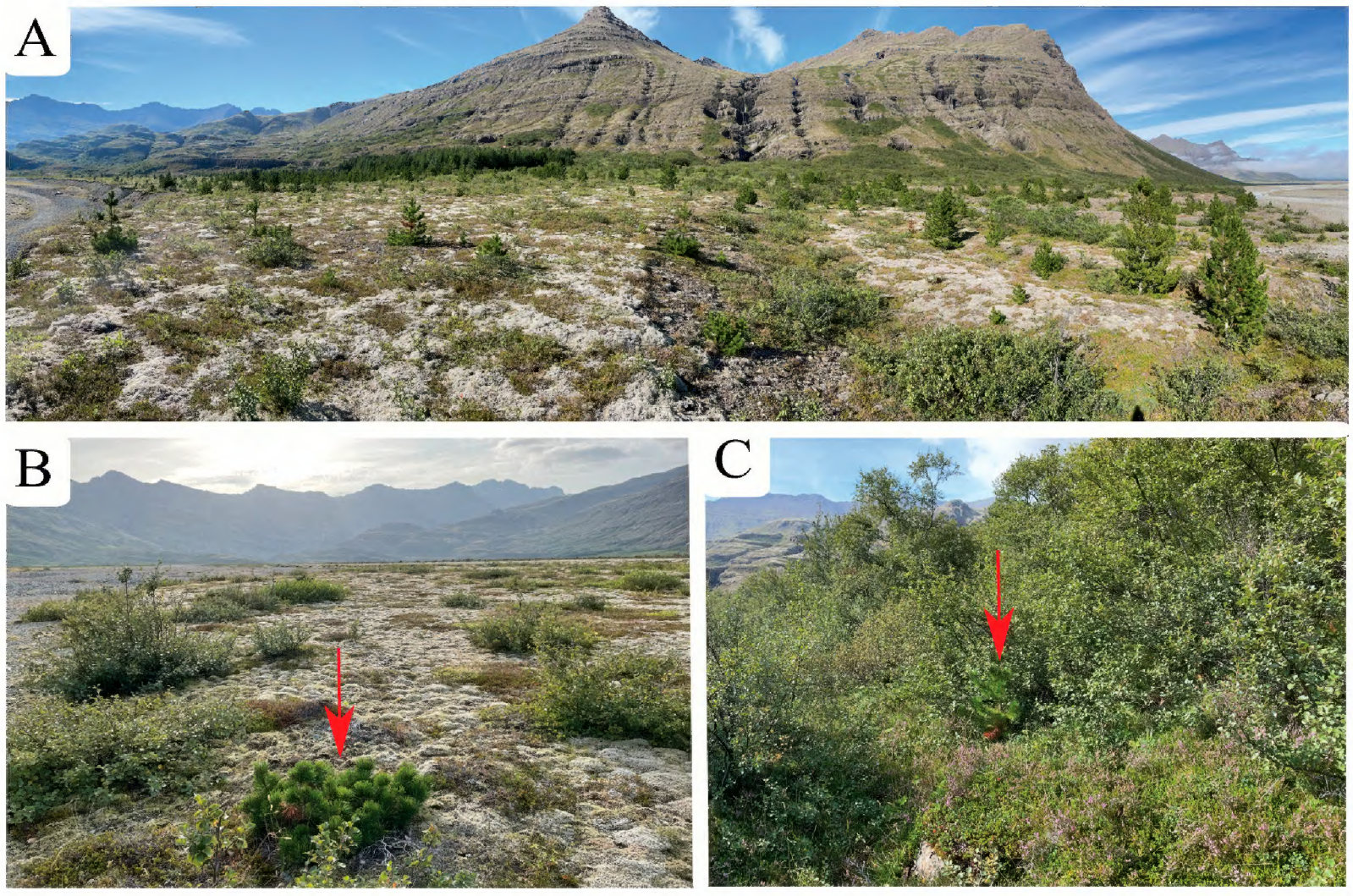

Figure 1. Heath vegetation already colonised by lodgepole pine (plantation can be seen in the distance) (**A**) and young lodgepole pines (marked with arrows) colonising moss heath in the valley mouth (**B**) and a birch woodland with dense vegetation cover (**C**).

Study design and field data

Systematic mapping of decadal-scale distribution changes

Field data were collected in 2010 (Guðmundsdóttir 2012) and 2021, using the same methods to ensure the comparability of data. The methods used were based on Langdon et al. (2010).

Guðmundsdóttir (2012) laid out a series of 24 2 m wide and 100 m long transects radiating at 10 m intervals southwest to southeast from the edge of the 1961 plantation fence. Two transects were excluded as their orientation was miscalculated and they crossed over to neighbouring transects. Each transect was divided into 10 m segments. In each segment, all lodgepole pines were recorded with their GPS coordinates. In 2021, transects used by Guðmundsdóttir were employed to remap lodgepole pine. The transects were lengthened beyond the original 100 meters to cover the newly colonised areas, extending to the banks of the Kaldakvísl River, with an average length of 153 metres. In addition, the total percentage of vegetation cover was recorded for each transect section.

Landscape-scale distribution

In September 2021, the distribution of lodgepole pine within Steinadalur was systematically surveyed and plants mapped using GPS coordinates in order to estimate the extent of occurrence (EOO) of the population (Wilson et al. 2014). The survey boundaries were set by the mountains bordering the valley to the north and south, to the west by the Dalsá river canyon and to the east by the expansive opening of the valley onto the Suðursveit plain. The survey area, approximately 5 km^2 in size, was systematically covered by two researchers. However, some inaccessible or hazardous areas were excluded from the survey. Due to the substantial increase in pine distribution since 2010 and the aerial extent of the valley, our survey should be regarded as a conservative estimate of the total spread area. GPS co-ordinates were recorded on: Trimble-R8 and GPSmap62s. All collected geographical data were handled in QGIS (QGIS Development Team 2024).

Vegetation sampling

Ten 0.5 × 0.5 m quadrats were randomly placed within three distinct vegetation types: lodgepole pine plantation, uninvaded heathland (located south of the plantation, within the same area as the transects), and uninvaded birch forest. We recorded all vascular plant species present and estimated both total plant cover and cover for each vascular plant species using the Braun-Blanquet scale (Braun-Blanquet 1932). Species concepts and nomenclature follow Wasowicz (2020).

Data analyses

Lodgepole pine density and spread

The density of lodgepole pine was calculated for each 10 m section of all transects and expressed as the number of trees per m^2. Subsequently, the mean density along all transects was calculated. Changes in density (2010–2021) were mapped and visualised using QGIS (QGIS Development Team 2024).

To calculate the EOO we used the minimum bounding geometry algorithm implemented in QGIS (QGIS Development Team 2024) to calculate a convex hull which covers the whole layer extent for each data set, i.e. collected in 2010 and in 2021 (Wilson et al. 2014). The resulting polygons were used as an approximation of the EOO.

To calculate the rate of spread we converted the outer lines of the convex hull to point layers with the density of 1 point per meter, using the geometry to points algorithm implemented in QGIS (QGIS Development Team 2024). Then the minimum distance from the previous extent geometry for each such point was calculated using the distance to the nearest hub (points) algorithm implemented in QGIS (QGIS Development Team 2024). The resulting distances were used as an approximation of the rate of lodgepole pine spread.

The outer periphery of the polygons, being the result of the previous step of the analysis (see above), were changed into point layers with the density of 1 point per meter, using the geometry to points algorithm implemented in QGIS (QGIS Development Team 2024). These points were used to extract the elevation values from an ArticDEM v3.0 elevation model (Porter et al. 2018). The difference between the highest values of elevation for each dataset served as an approximation of the rate of the vertical spread.

Model fitting

We assessed the relationship between the species' total colonised area and time, and the total number of trees in the transects over time by fitting linear and non-linear models to our observations. Considering the nature of the process (plant invasion) and well-documented spread patterns, the exponential function was likely the most suitable choice. For fitting both linear and exponential models, we employed the nonlinear least squares regression using the *nls* function in R 4.4.1 (R Core Team 2024).

The linear model assumed a constant growth rate over time expressed as:

$$A(t) = a + b \times (t\text{-}1985)$$

where:

$A(t)$ is the area occupied by the lodgepole pine (or tree count) at time t
a is the y-intercept, representing the initial area in 1985,
b is the slope of the line, representing the rate of change of the plant area over time
t represents the calendar year.

Whereas the exponential model was:

$$A(t) = A_0 \times e^{r \times (t-1985)}$$

where:

$A(t)$ is the area occupied by the lodgepole pine (or tree count) at time t
A_0 is the initial area of spread in 1985
e represents Euler's number
r is the growth rate
and t represents the calendar year.

The fitting process involved optimising the model parameters to minimise differences between predicted and observed values. Model comparison was performed using three metrics, i.e. residual standard error, variance explained and the Akaike Information Criterion (AIC), providing insights into the goodness of fit and model complexity.

Estimation of species richness

Community level (alpha) species richness and diversity were compared for the three different vegetation types (uninvaded birch woodland, uninvaded heath and lodgepole pine plantation). Statistically significant differences between vegetation types were assessed using the Kruskal-Wallis test and pairwise comparisons using Dunn´s test with Bonferroni correction for p-values, at $\alpha = 0.05$.

Results

Decadal changes in EOO and population growth

The extent of occurrence (EOO) of lodgepole pine in Steinadalur expanded nearly tenfold over just a decade, growing from 0.25 km^2 in 2010 to 2.39 km^2 in 2021 (Fig. 2). Over the same period, the number of lodgepole pine individuals recorded across 22 transects increased dramatically, rising from 429 in 2010 to 3,315 in 2021—an almost eightfold growth. Similarly, the average density of lodgepole pine across all transects rose by over sevenfold, from 0.06 plants/m^2 in 2010 to 0.46 plants/m^2 in 2021. Original data and fitted curves can be found in Suppl. material 1.

The extent of occurrence (EOO) and indices of population growth of lodgepole pine (measured by tree count and mean tree density in transects) were analysed using both linear and exponential models. Exponential models consistently outperformed linear ones, showing lower residual standard error, higher explained variance, and lower Akaike Information Criterion (AIC) values (Table 1). Consequently, the observed trends are best represented by an exponential growth model.

The mean annual spread rate of lodgepole pine increased significantly, from 8.5 ± 2.4 m/year during 1985–2010 to 61.6 ± 40.2 m/year between field studies (2010–2021). Local rates of spread also shifted, with minimum rates rising from 3.4 m/year in 2010 to 8.3 m/year in 2021, and maximum rates increasing from 13.4 m/year to 119.3 m/year over the same period (Fig. 3A). Elevational spread also progressed, with the highest recorded elevation rising from 70 m in 1985 to 116 m in 2010, and 170 m in 2021. Meanwhile, the lowest recorded elevations shifted downward, from 44 m in 1985 to 38 m in 2010, and 25 m in 2021 (Fig. 3B).

Spatial patterns in lodgepole pine density (2010–2021)

Lodgepole pine density exhibited clear spatial gradients in both 2010 and 2021, with the highest densities near the original plantation and decreasing with distance. In 2010, peak densities of 0.5–0.6 plants/m^2 were observed primarily within 100 m of the plantation edge (Fig. 4). By 2021, these densities had increased by an order of magnitude, with plants recorded farther from the edge, often in areas previously uncolonised.

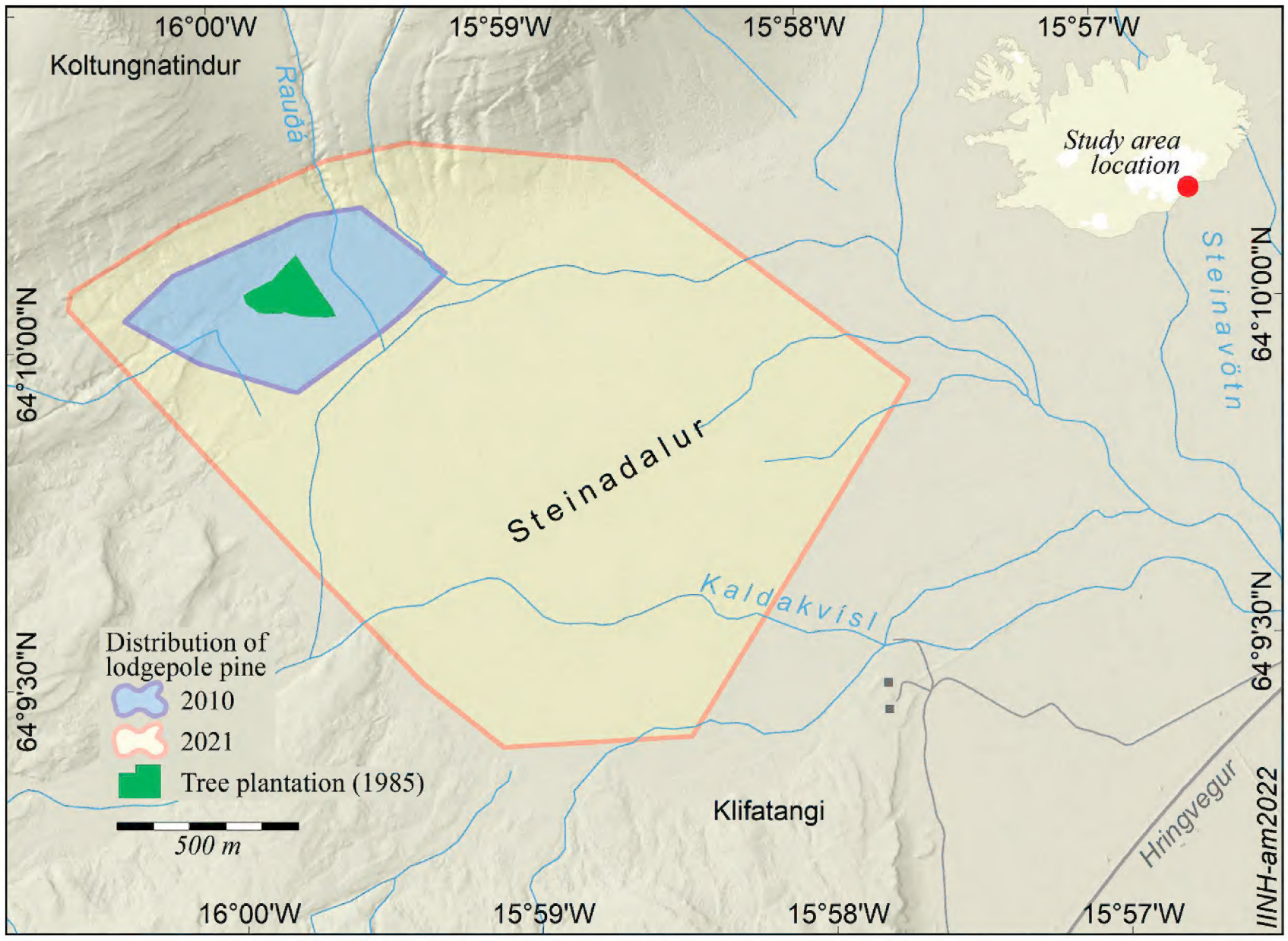

Figure 2. The extent of occurrence (EOO) of lodgepole pine (*P. contorta*) in Steinadalur (1985–2021).

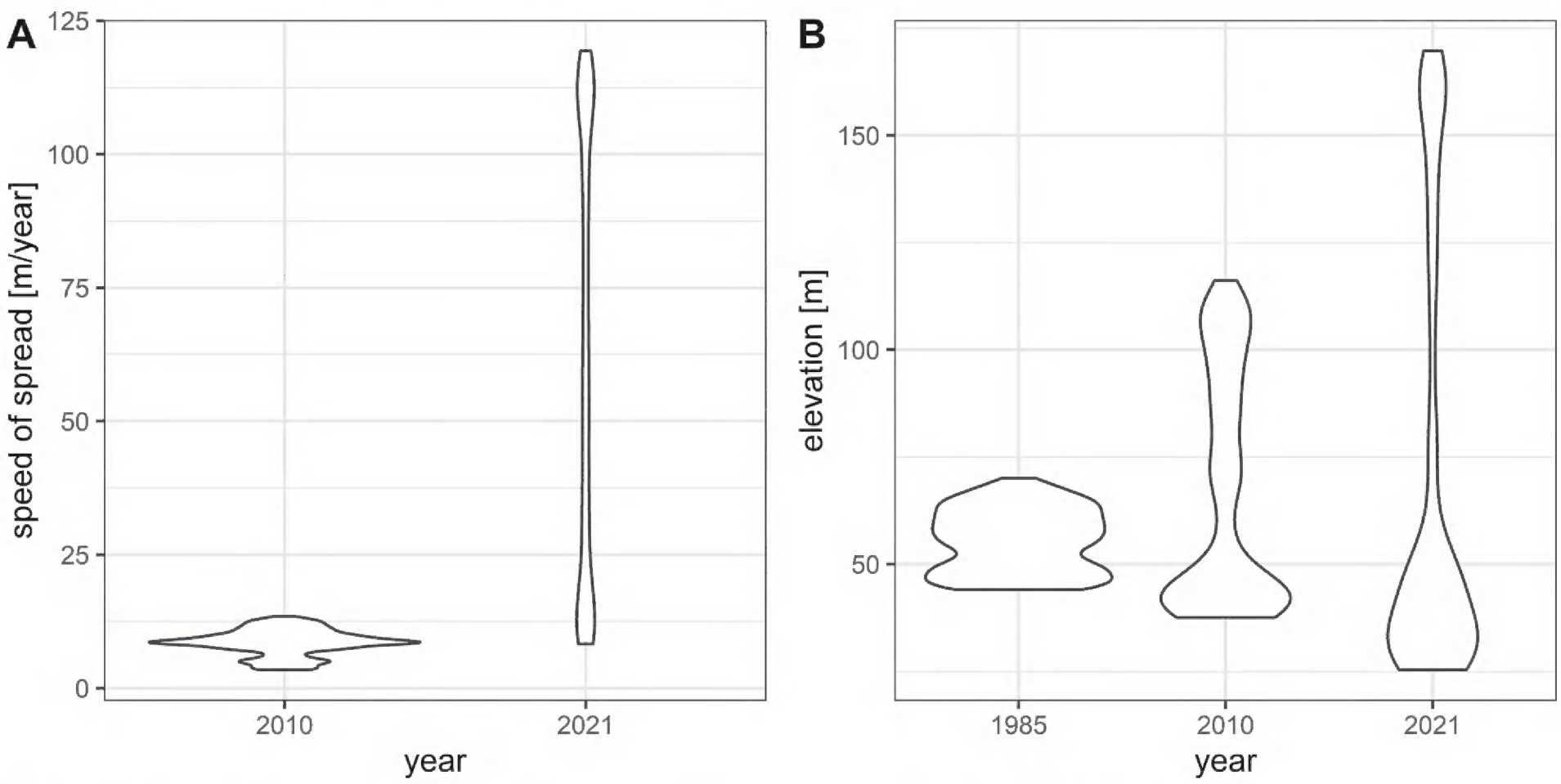

Figure 3. The rate of horizontal (**A**) and vertical (**B**) spread of lodgepole pine in Steinadalur (SE Iceland).

Lodgepole pine colonisation occurred across various native habitats in Steinadalur, including dwarf shrub and *Carex bigelowii* heathland, mossy *Racomitrium* grass heath, birch forest, and early-succession open habitats formed by unconsolidated fluvial sediments.

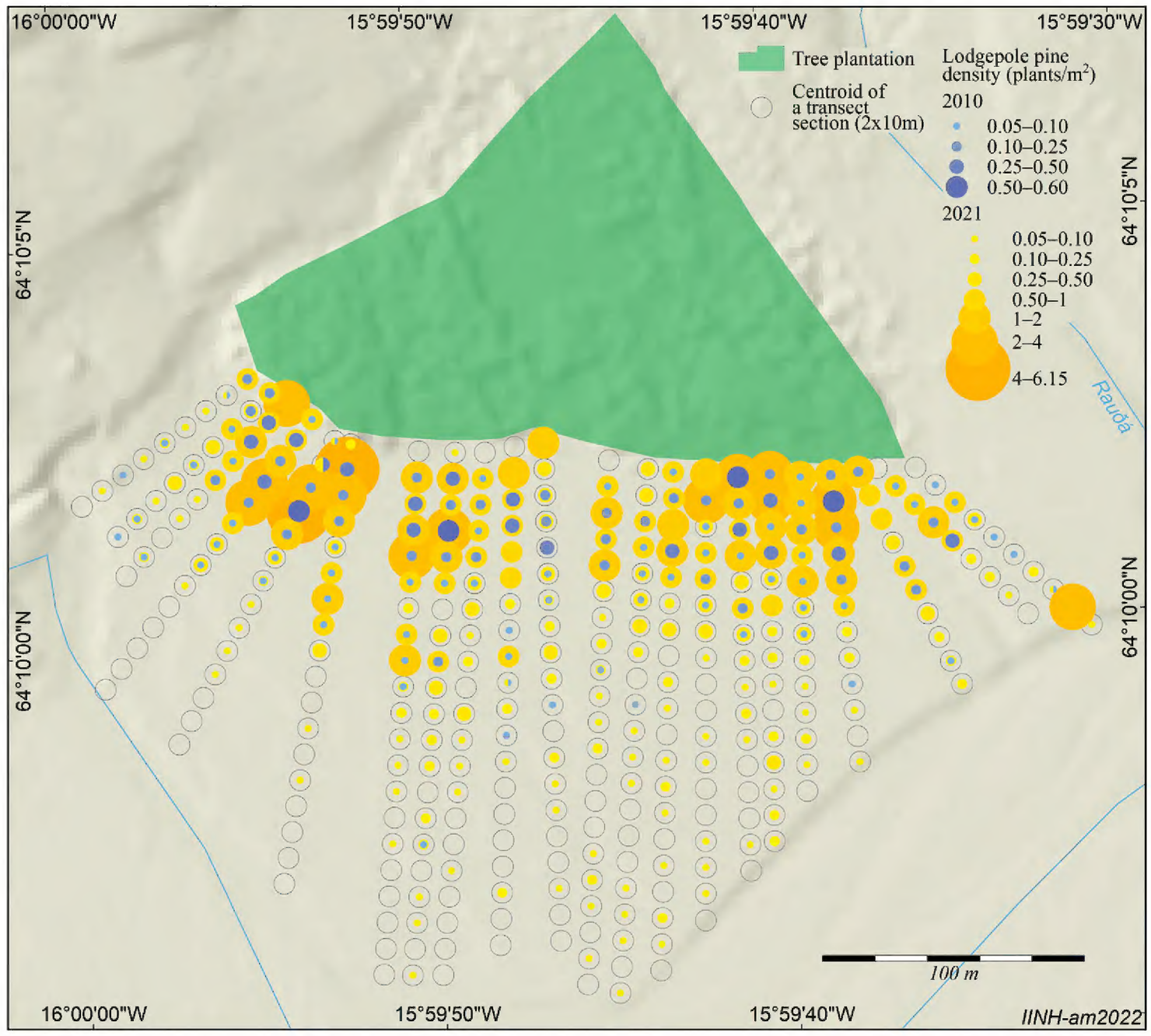

Figure 4. Changes in lodgepole pine densities along the 22 transects in Steinadalur (SE Iceland).

Table 1. Comparison of linear and exponential models using residual standard error, variance explained, and AIC.

		Std. Err.	Var. Expl.	AIC
Area	linear model	1.1	0.64	11.9
	exponential model	1.6×10^{-3}	0.99	-27.5
Number of trees	linear model	1492.0	0.66	55.1
	exponential model	3.1	0.99	18.0
Mean density	linear model	15.9	0.66	1.6
	exponential model	1.8×10^{-5}	0.99	-33.4

Vascular plant species richness and diversity across vegetation types

Vascular plant species richness was lowest in lodgepole pine plantations, with both birch woodlands and heathlands supporting significantly more species (Fig. 5A). Statistical analysis confirmed these differences (Kruskal-Wallis rank sum test: $H = 24.31$, $df = 2$, $p = 5.27 \times 10^{-6}$). Pairwise comparisons using Dunn's test revealed significant differences between birch and pine ($p = 2.73 \times 10^{-6}$) and between heath and pine ($p = 0.02$), but not between birch and heath ($p = 0.10$).

Similar patterns were observed in Shannon diversity index values, which were lowest in lodgepole pine plantations (Fig. 5B). Differences between vegetation types were statistically significant (Kruskal-Wallis rank sum test: $H = 25.46$, $df = 2$, $p = 2.96 \times 10^{-6}$). Dunn's test showed significant differences between all vegetation types: birch vs. heath ($p = 0.03$), birch vs. pine ($p = 1.35 \times 10^{-6}$), and heath vs. pine ($p = 0.049$).

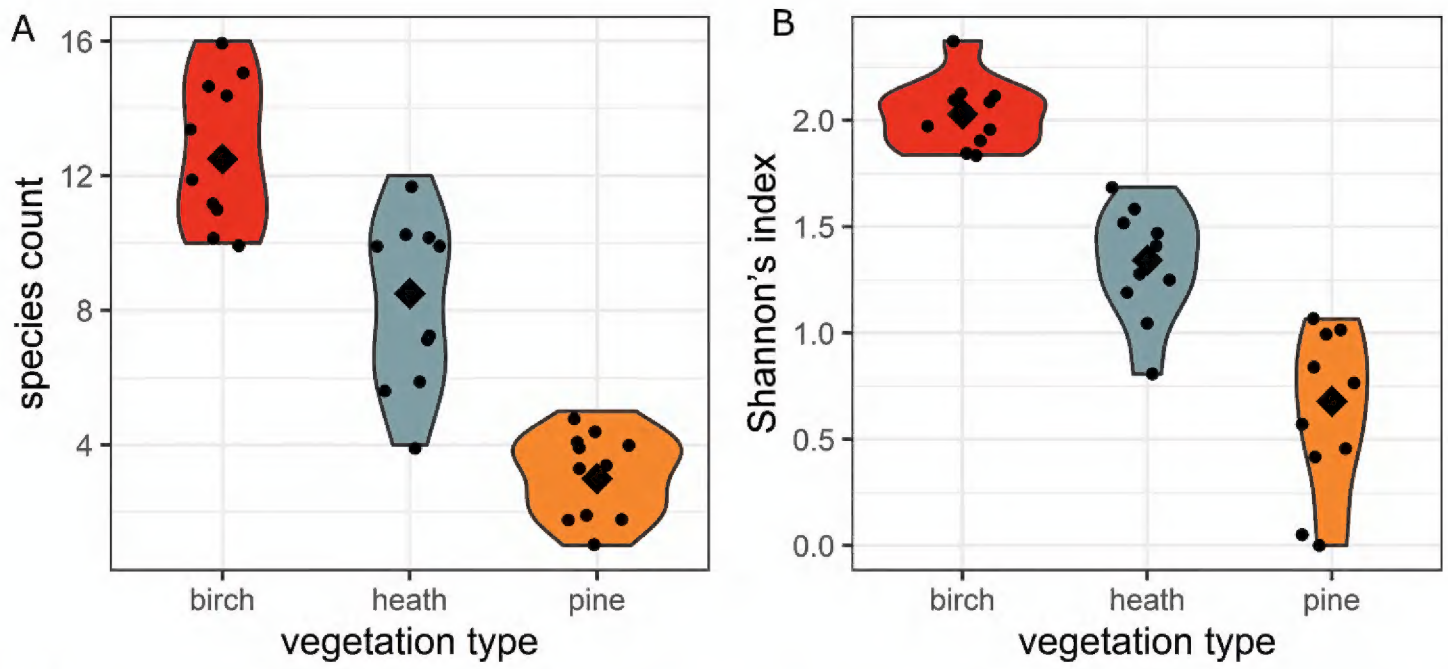

Figure 5. Violin plots showing the number of vascular plant species recorded in vegetation plots (**A**) and values of Shannon diversity index (**B**) in three different vegetation types: birch woodland, heath and lodgepole pine plantation. Points denote values of direct measurements, diamonds denote median value for each vegetation type.

Discussion

Patterns of population expansion and growth

The invasion process generally follows a predictable trajectory, irrespective of taxonomic identity of the species (Shigesada and Kawasaki 2001). Following establishment, there is typically a lag period with slow spread, after which the invader enters an exponential growth phase. This expansion continues until available space is saturated, at which point the spread rate levels off (Shigesada and Kawasaki 2001; Arim et al. 2006).

Metrics for lodgepole pine in Steinadalur reflect an accelerating spread, particularly over the last decade. The mean spread rate increased nearly eightfold, from 8.5 m/year over the first 25 years (1985–2010) to 61.6 m (2010-2021). Occupied area expanded almost tenfold, and tree density in belt transects increased nearly eightfold between 2010 and 2021. These rates align with models of exponential, not linear, growth, strongly suggesting that lodgepole pine in Steinadalur has entered the exponential growth phase.

This raises the question: are these patterns primarily driven by Malthusian population growth in unsaturated environment, or do environmental changes, such as climate warming, play a role? Across Europe, the Normalized Difference Vegetation Index (NDVI) has shown a positive trend over the last 30 years (Eisfelder et al. 2023). In Iceland, this trend is pronounced in the west and north but weaker in the east and southeast. These changes are attributed to higher temperatures, increased rainfall, and reduced summer grazing by free-range sheep (Raynolds et al. 2015), although disentangling causal factors remains challenging. Since the 1980s, Iceland's mean temperatures have risen by 0.47 °C per decade, about three times the global average (Hanna et al. 2004; Björnsson et al. 2018).

Steinadalur, located in the southeast of the country, benefits from a milder climate, longer growing season, and higher rainfall than other regions (unpublished data from the Icelandic Met Office). Warm temperatures likely facilitated the lodgepole pine's growth and expansion, and ongoing warming trends are expected to favour it further. Sheep graze in Steinadalur during summer but their impact on the pine has not been documented. The species' altitudinal range, reaching 170 m by 2021, indicates that temperature constraints are unlikely to limit its spread.

Susceptibility of native ecosystems and ecosystem-level impacts

The Steinadalur case study illustrates that lodgepole pine can colonise not only eroded or sparsely vegetated land but also areas with closed vegetation. The lodgepole pine plantation in Steinadalur was established in areas previously occupied by heath or birch woodland. In Iceland, birch woodlands and forests represent the most structurally complex native vegetation. These birch ecosystems vary from old forest fragments with tall, monocormic trees and dense ground layers of graminoids and broad-leaved dicots to open woodlands dominated by polycormic shrub-like birch and dwarf shrubs (Ottósson et al. 2016). According to our results, lodgepole pine is likely to invade most low-stature vegetation types, particularly in warmer lowland regions of Iceland.

Native lodgepole pine forests in North America are characterised by limited undergrowth (Eyre 1980; Perry et al. 2008). When planted outside their native range, lodgepole pine consistently reduces the species richness and diversity of native vegetation (Ledgard and Paul 2008; Urrutia et al. 2013). In New Zealand, vascular plant species richness in grasslands invaded by lodgepole pine declined from 38 to seven species within 20 years (Ledgard and Paul 2008), with none of the remaining species being native. Similarly, in British Columbia, the oldest lodgepole pine forests exhibited the lowest plant species diversity (Sullivan 2004). At the ecosystem level, lodgepole pine invasion constitutes a major state shift. Dense, fast-growing stands drastically reduce sunlight penetration, gradually eliminating shade-intolerant species associated with subarctic heathlands, grasslands, and birch woodlands. In Steinadalur, although based on a small sample size, comparisons of vegetation types strongly suggest significant impacts on native species composition and vascular plant species richness, likely due to light limitation as dense canopies develop, eliminating low-growing and light-demanding species. The significant reductions in species richness observed are clear indications of profound ecosystem changes.

A specific concern in Iceland is the impact of lodgepole pine on native bird populations, particularly wading birds. Iceland is a critical breeding area for waders in Europe (Gunnarsson 2020). Pálsdóttir et al. (2022) documented significant declines in wader densities near plantation edges, likely indicating population losses rather than shifts in habitat use. According to their study, estimated losses from plantations may already amount to tens of thousands of birds, underscoring the far-reaching impacts of tree plantations on Iceland's ecosystems.

In addition to biodiversity loss, lodgepole pine invasion can result in reduced surface streamflow, heightened fire risks, soil erosion following clearcutting, destabilized riverbanks, and a decline in recreational opportunities and grazing land for livestock (De Wit et al. 2001). Managing invasive woody species like lodgepole pine is challenging, with removal often failing to restore ecosystems to their previous state (Panetta 2012; Sapsford et al. 2020). Conifer invasions also alter soil chemistry, hydrology, and fungal communities, potentially increasing soil CO_2 emissions and reducing albedo, which exacerbates warming in temperate and cold regions (Popkin 2019; Nuñez et al. 2021).

Should lodgepole pine be considered invasive in Iceland?

Most criteria for assessment of vulnerability to IAS apply to Iceland: 1) it is an isolated oceanic island (Pyšek et al. 2020; Dueñas et al. 2021), 2) has a natural disturbance regime that periodically creates open ground, and 3) native ecosystems that suffered severe destruction and degradation in the wake of human settlement

(Richardson et al. 1994; Barrio and Arnalds 2022). Finally, the indigenous flora mostly comprises low-growing shrubs and herbs, i.e. growth forms very different from that of the invader (here lodgepole pine, Richardson and Bond 1991). Among the many invasive strengths of lodgepole pine are the high dispersibility of its seeds and frequent copious seed output (Richardson et al. 1994). The future spread of lodgepole pine in Iceland is likely to be significantly accelerated by the widespread practice of establishing numerous small plantation projects across the country's lowland regions.

Lodgepole pine in Iceland fulfils the scientific definitions of an invasive species. Its spread rates, exceeding 100 m in less than 50 years in Steinadalur, and significant negative impacts on biodiversity, comply with IAS criteria (Richardson et al. 2000; Pyšek et al. 2004). Established outside its original plantation for approximately 35–40 years, it has reached distances of nearly 3 km and demonstrated exponential growth. Research is needed to understand its effects on trophic networks, belowground biota, bird and mammal populations, and landscape-scale homogenization. Regional-scale studies are critical, as lodgepole pine appears to be spreading across Iceland, even in colder northern regions (Brynjólfsson 2022).

Implications for management and policy in Iceland

Perceptions of the reality and magnitude of the threat invasive species may pose are known to vary greatly among social groups (García-Llorente et al. 2008), not least when benefitting stakeholders differ from those concerned with negative impacts (Novoa et al. 2024). The failure of many countries to implement successful management and control practices has been attributed to little public and political awareness (Bertolino and Genovesi 2003), and lack of cohesion between scientific researchers, the commercial sector, and policy makers (Stokes et al. 2006). The emerging consensus is that effective management of invasive non-native species largely depends on the active support and collaboration of all relevant stakeholders (e.g. Brundu et al. 2020).

In Iceland, attitudes toward potentially invasive conifers are deeply polarised, with a sharp divide between those anticipating direct benefits and those expressing concerns about environmental impacts. Academics, biologists at state and regional institutes and environmental associations, have warned against indiscriminate use of introduced species and the widespread planting of lodgepole pine (Von Schmalensee 2010; Bjarnason et al. 2023; Jónsdóttir 2023). In contrast, the forestry sector, as well as national and regional afforestation associations have remained staunch advocates of continuing large-scale planting of lodgepole pine and dismiss it as a potential threat to Iceland's biodiversity. The statements and arguments presented in Icelandic media and forestry publications reflect this divide. Claims include rejecting the term "invasive alien species" as invalid and arguing that concerns about invasive species are logically flawed (Sigurgeirsson 2014). Some maintain that lodgepole pine is not invasive (Eysteinsson 2021), that trees cannot become invasive, or that unwanted trees can be easily removed (Eysteinsson 2019). Invasion research has been portrayed as pseudoscience driven by nationalism (Sigurgeirsson 2005; Gardarsson 2022; Eysteinsson 2023). The most pressing task for Iceland is to enhance knowledge through rigorous scientific studies that provide a solid foundation for assessing the risks and long-term consequences of large-scale lodgepole pine cultivation. This evidence should facilitate informed dialogue among stakeholder groups.

Conclusion

This study reveals that lodgepole pine in Steinadalur has entered an unregulated exponential growth phase, replacing natural ecosystems with dense, species-poor woodlands. With no effective competitors in Iceland, lodgepole pine fulfils IAS definitions and poses severe threats to native ecosystems. Addressing its spread requires urgent management and further research on its long-term ecological impacts. As an oceanic, sub-Arctic island with limited native tree flora and degraded ecosystems, Iceland is exceptionally vulnerable to IAS. Indigenous birch forests, covering only 1.5% of Iceland's land area, are unlikely to resist lodgepole pine invasion. The species' ability to form self-perpetuating communities in the absence of native competitors poses a long-term threat to Iceland's ecosystems, landscapes, and biodiversity.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Conceptualization: PW. Data curation: PW. Formal analysis: GÓ, PW. Funding acquisition: PW. Investigation: GÓ, PW. Methodology: GÓ, PW. Project administration: PW. Resources: PW. Supervision: PW. Validation: PW. Visualization: PW. Writing - original draft: PW, ÞEÞ, GÓ. Writing - review and editing: GÓ, PW, ÞEÞ.

Author ORCIDs

Pawel Wasowicz https://orcid.org/0000-0002-6864-6786
Guðrún Óskarsdóttir https://orcid.org/0000-0001-8128-8306
Þóra Ellen Þórhallsdóttir https://orcid.org/0000-0003-2946-5963

Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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Supplementary material 1

Climatic diagrams and data for the measured variables, including EOO, tree count, and tree density

Authors: Pawel Wasowicz, Guðrún Óskarsdóttir, Þóra Ellen Þórhallsdóttir

Data type: pdf

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